

TWO NEW CRABS, *HOMOLOPSIS WILLIAMSI* AND
HOMOLOPSIS CENTURIALIS (CRUSTACEA: DECAPODA),
FROM THE WESTERN INTERIOR CRETACEOUS
OF THE UNITED STATES

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Abstract.—A single specimen representing a new species of a Cretaceous homolid crab occurs in the *Linuparus* faunal association of the Turonian Carlile Shale on the northern and eastern flanks of the Black Hills Uplift in South Dakota and Wyoming. *Homolopsis williamsi* is characterized by a quadrate, relatively flat carapace with well-developed grooves and prominent tubercles on the posterolateral margins. The specimen is preserved as an internal carapace steinkern enclosed in an apatite concretion associated with shell fragments of the bivalve mollusk *Inoceramus*. Another specimen representing a second new species of homolid crab was collected from the Heart Tail Ranch decapod association of the mid-early Campanian Gammon Ferruginous Member of the Pierre Shale on the northern flank of the Black Hills Uplift in Butte County, South Dakota in 1989. This new species, *Homolopsis centurialis*, is characterized by a more typical quadrate carapace with well defined grooves and tumid lobes surmounted by boss-like protuberances. The specimen is preserved in an apatite concretion in which the sides of the crab are somewhat splayed outward by vertical compaction. Review of the stratigraphic and geographic distribution of *Homolopsis* shows a pattern of development along the northern margin of the Tethys Seaway in western and northern Europe as well as in Australia during the Early Cretaceous and immigration into, and evolution in, the opening Atlantic and flooded Western Interior seaways of North America and northern Europe during the Late Cretaceous.

The apatite-preserved, decapod-rich fauna of the Pool Creek Shale Member of the Carlile Shale described by Bishop & Williams (1986), consists of the lobsters *Linuparus canadensis* (Whiteaves 1885), undescribed species of *Hoploparia*, and *Palaeonephrops*, and the crabs *Necrocarcinus olsonorum* Bishop & Williams, 1991, and *Homolopsis williamsi*, new species, in association with abundant worm, bryozoans, bivalves, cephalopods, vertebrates, and a few other taxa. The decapod assemblage is confined vertically to 3 m of shale, preserved in burrowed and pelleted apatite concretions, and has been traced continuously along strike for approximately 117 km, and down dip for 8 km, a distribution of at

least 936 km². The Carlile Shale *Linuparus* assemblage represents the preserved fraction of an opportunistic decapod-worm association which periodically appeared in the Western Interior Cretaceous in response to mass killings and nutrient rains onto the substrate surface (Bishop 1986a).

Collecting in the Carlile Shale *Linuparus* Assemblage Zone (Bishop & Williams 1986), yielded a single crab (Figs. 1, 2) not assignable to any existing species. This specimen is herein described and named *Homolopsis williamsi*.

A second new species of *Homolopsis* (Figs. 3, 4) was discovered in the lower Pierre Shale while collecting with Austin B. Williams on the Heart Tail Ranch during the summer of

1989. This specimen was immediately recognized as a *Homolopsis* because of the typical, well differentiated carapace with tumid lobes surmounted by a typical complement of boss-like spines. This specimen was collected from the Heart Tail Ranch Assemblage (Bishop 1985, 1987), which is also a decapod-rich, apatite-preserved decapod-worm association (Bishop 1987). This fauna consists of eight decapod species associated with ubiquitous worm burrows and fecal pellets, abundant baculitid cephalopods, scarce rudistid mollusks (*Titanosarcolithes*), thin-shelled oysters (*Ostrea*), gastropods (*Trachytriton* and *Graphidula*), and abundant trace fossils. The decapod portion of the fauna, which now consists of 1644 specimens, is dominated by the decapods *Protocallianassa russelli* Bishop, 1985 (74.0%), *Necrocarcinus davisi* Bishop, 1985 (14.6%), and *Hoploparia mickelsoni* Bishop, 1985 (9.5%) but includes also *Raninella oaheensis* Bishop, 1978, *Dioratiopus hearttailensis* Bishop, 1985, *Xanthosia occidentalis* Bishop, 1985 (Bishop 1991), *Rugafarius frederichi* Bishop, 1985, *Dromiopsis kimberlyae* Bishop, 1987, and *Homolopsis centurialis* new species. The low rate of incidence of *H. centurialis* in the Heart Tail Ranch Assemblage (1 specimen in 1644) indicates the probability of finding additional specimens is very small. The description of *H. williamsi* and *H. centurialis* expands the North American record for *Homolopsis*, and facilitates the review of the stratigraphic and paleogeographic distribution of this genus.

Type specimens of the new species are deposited in the collection of the Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota 57701.

Systematic Paleontology

Subsection Archaeobrachyura Guinot, 1977

Family Holmolidae Bell, 1863

Genus *Homolopsis* Bell, 1863

Type species. — *Homolopsis edwardsi* Bell, 1863, from the Albian of Folkstone, Kent.

Diagnosis. — Carapace more or less rectangular, ranging from much longer than wide to slightly wider than long, flat to moderately arched, lobes often tumid; moderately to highly sculptured with prominent, transverse, cervical and oblique branchiocardiac grooves passing anterior of epigastric lobes which usually form widest part of carapace. Orbital margins long, diverging backward, orbits subquadrate. Lateral margins parallel to slightly convergent posteriorly. Posterior margin straight to concave, often bordered by thin, raised rim. Rostrum triangular, downturned. Orbital regions open, eyestalk resting against hepatic lobe. Legs long, narrow, spinous. Chelipeds subequal, robust, often ornamented with longitudinal ridges and tubercles.

Discussion. — *Homolopsis* is known (see Fig. 6) from the Early Cretaceous of Europe and Australia, being found in the Neocomian of France (*Homolopsis tuberculata* Van Straelen 1936). *Pithonoton planum* Van Straelen, 1936, from the Neocomian of France, was reassigned to *Homolopsis* and *Prosopon schneideri* Stolley, 1924, from northern Germany, was questionably assigned to *Homolopsis* by Wright & Collins (1972). *Homolopsis* occurs in the Albian and Cenomanian of Great Britain (*H. glabra* Wright & Collins, 1972, *H. brightoni* Wright & Collins, 1972, and *H. edwardsi* Bell, 1863). *Homolopsis* is known from the Late Cretaceous of northern Germany and Scandinavia in the lowest Senonian (*H. gibbosa* Schlüter, 1868), the upper lower Senonian (*H. schlueteri* Beurlen, 1928), and from the Maastrichtian and Danian (*H. transiens* Seegerberg, 1900). In North America, *Homolopsis* is known from the Late Cretaceous on the northern Atlantic Coastal Plain in the mid-early Campanian (*H. atlantica* Roberts, 1962 and *H. dispar* Roberts, 1962) and from the Western Interior Seaway from the Turonian (*H. williamsi*, new species), mid-early Campanian (*Homolopsis centurialis*, new species), and the Maastrichtian (*H. punctata* Rathbun, 1917).

Two problematic species have been de-

scribed from Australia: *H. etheridgei* (Woodward, 1892) which probably is better assigned to *Zygastrocarcinus* Bishop, 1983 and *Homolopsis spinulosa* Glaessner, 1980, which, although clearly a homolid, is sufficiently different morphologically to warrant eventual assignment to a new genus.

Homolopsis williamsi, new species

Figs. 1, 2, 5a

Diagnosis. — Carapace rectangular, longer than wide, flat, deeply grooved with prominent cervical and branchiocardiac grooves. Lateral margins convergent posteriorly, posterolateral margins strongly tuberculate. Regions smooth, non-tumid.

Types. — Holotype, SDSM 11,014.

Occurrence and preservation. — The specimen of *H. williamsi* was collected on land belonging to Norman Durr in the SE $\frac{1}{4}$, NE $\frac{1}{4}$, section 15, T. 9 N, R. 2 E, Butte County, South Dakota. The dorsal surface of the specimen, preserved as an internal steinkern enclosed in an apatite concretion along with several plates of prisms of the bivalve mollusk *Inoceramus*, is crushed slightly downward into the visceral cavity. Cross sections of some appendages are visible on the exterior surface of the concretion, and the dorsum of the steinkern is slightly corroded and therefore does not exhibit traces of the external ornamentation of the carapace.

Description. — Carapace rectangular, longer (13.42 mm) than wide (12.53 mm), widest at anterolateral processes approximately $\frac{1}{4}$ distance from front. Anterolateral margins oblique, long; lateral margins somewhat convergent posteriorly, slightly curved; posterolateral edge fairly angular, ornamented by 4–5 large tubercles anteriorly; posterior margin concave. Dorsum flat, regions (as defined by Wright & Collins 1972:fig. 1) well delineated by deep, distinct grooves. Cervical groove deeply incised from gastric ridge nearly to edge of dorsum, faintly visible across gastric ridge separating dorsum into anterior portion (cephalic arch of

Milne-Edwards as defined by Bell 1858:iii) and posterior portion (scapular arch of Milne-Edwards as defined by Bell 1858:iii). Groove delineating mesogastric region deep and well defined, sweeping backward and outward, crossing cervical groove and extending onto mesobranchial lobe before looping inward along posterior margin of urogastric lobe and anterolateral margin of cardiac lobe (forming the epimeral peninsulas), then joining brachiocardiac furrow and sweeping outward and forward to dorsal edge. A fainter groove branches off proximal brachiocardiac groove to delineate posterolateral edges of cardiac lobe which is separated by a shallow transverse furrow from intestinal lobe. Anteriorly, faint grooves separate protogastric and hepatic lobes. Protogastric lobe separated by very faint groove into narrow proximal area and larger distal area surmounted by tiny tubercles. Hepatic lobe consists of large proximal area separated by faint groove from smaller distal area inflated into a small boss surmounted by single tiny tubercle. Mesogastric lobe has a long, narrow anterior tongue extending onto rostral area apparently downturned into bifurcated rostrum, and abruptly widens posteriorly into triangular mesogastric lobe which, being weakly separated from urogastric lobes, forms a rather urn-shaped combined area.

Scapular arch well delimited by deep furrows into gastric ridge and branchial lobes. Gastric ridge barely differentiated by cervical furrow between mesogastric and urogastric lobes but well delimited by brachiocardiac groove laterally. Cardiac and intestinal lobes more or less fused and nearly separated from urogastric lobe by deep groove. Branchial region differentiated into large, posterior metabranchial lobe and smaller, anterior mesobranchial-epibranchial lobe. Mesobranchial lobe faintly separated from distal epibranchial lobe by very shallow groove splitting off cervical groove. Epibranchial lobe inflated and angular, forming epibranchial angle and widest portion of carapace accentuated by curvature



Fig. 1. Reconstruction of carapace of *Homolopsis williamsi*, new species, dorsal view.

of cervical furrow around inner and anterior margin of epibranchial lobe. Two tiny marginal tubercles on dorsal edge of the epibranchial lobe in line with tubercles on posterolateral margin. Mesobranchial lobe somewhat separated into proximal and distal areas by shallow groove which is posterior extension of cervical furrow near lateral edge of urogastric lobe. Metabranchial lobe mostly flat but with subtle ridge proximally, and 4 marginal tubercles just posterior to intersection of branchiocardiac furrow and dorsal edge.

Carapace crushed along linea homolica which lies just inside dorsal shield lateral margins, extending from posterior margin to just outside orbits, slightly arcuate inward.

Etymology.—This species is named in honor of my colleague and friend, Austin B. Williams, who has dedicated so much of his professional life to the study of the decapod crustaceans.

Comparison.—*Homolopsis williamsi* is easily distinguished from its North American congeners *Homolopsis centurialis* n. sp. (Fig. 5b), *H. atlantica* (Fig. 5d), *H. dispar* (Fig. 5e), and *H. punctata* (Fig. 5c), and nearly all other homolopsids because of its lack of tumid lobes and lack of boss-like ornamentations which are characteristic of



Fig. 2. Photograph of holotype of *Homolopsis williamsi*, new species, dorsal view, embedded in apatite concretion. (Scale = 1 cm)

virtually every other species of *Homolopsis* except for *H. glabra*. *Homolopsis williamsi* most resembles *H. glabra* from which it is distinguished by being more rectangular and relatively longer, by lacking the well-defined medial part of the cervical groove present in *H. glabra*, by lacking the well-defined distal epibranchial furrow present in *H. glabra*, and by possessing large tubercles on the posterolateral margin lacking in *H. glabra*.

Remarks.—The presence of *H. williamsi* in the *Linuparus* association from the Carle Shale reemphasizes the need for large collections of decapods from apatite-preserved decapod-rich assemblages. Only collections numbering in the hundreds or thousands are likely to have a significant chance of yielding scarcer faunal elements such as *H. williamsi*.

The preservation of a steinkern such as the holotype of *H. williamsi*, does not present a complete complement of morphologic information particularly on the exterior of the cuticle; however, the gross morphology preserved is adequate to define

this new taxon. The complete description of this crab's morphology must await a time when another specimen is found with preserved exoskeleton and appendages. Because this is a minor taxon in the *Linuparus* association (abundance of 0.06%), it is anticipated that another thousand specimens will have to be collected before we can find another specimen of *H. williamsi*. The breakage of the specimen parallel to the edges of the dorsal shield margins along the linea homolica is typical of the homolopsid crabs.

Homolopsis centurialis, new species

Figs. 3, 4, 5b

Diagnosis.—Carapace more or less rectangular, longer than wide, moderately arched, with oblique cervical and branchiocardiac grooves; lobes moderately tumid, moderately sculptured. Lateral margins parallel, slightly convergent posteriorly; posterior margin concave and sinuous. Rostrum triangular, downturned; orbital regions unknown. Anterior protogastric boss most distal; posterior medial metogastric boss small and posteriorly situated; cardiac region inflated, finely granulate, and transverse.

Types.—Holotype, SDSM 11,015.

Occurrence and preservation.—The specimen of *H. centurialis* was collected on the Heart Tail Ranch in the NW ¼, SE ¼, NE ¼ section 17, T. 11 N, R. 2 E, Butte County, South Dakota. The specimen, preserved in an apatite concretion, is crushed slightly and broken along the linea homolica with the carapace sides splayed outward into the plane of the carapace dorsum. External ornamentation is preserved on the cuticle.

Description.—Carapace rectangular, longer (13.9 mm) than wide (13.5 mm), widest at anterolateral processes approximately ⅓ length from front. Anterolateral margins oblique, long; lateral margins convergent posteriorly, nearly straight; posterolateral edge fairly angular, ornamented by 4 small

tubercles; posterior margin concave, sinuous. Dorsum slightly arched, regions (as defined by Wright & Collins 1972:fig. 1) well delineated by moderately deep, distinct grooves. Cervical groove present from gastric ridge nearly to edge of dorsum, faintly visible across gastric ridge separating dorsum into an anterior portion (cephalic arch of Milne-Edwards as defined by Bell 1858:iii) and posterior portion (scapular arch of Milne-Edwards as defined by Bell 1858:iii). Branchiocardiac groove incomplete, beginning at its junction with mesogastric groove, crossing cervical groove and sweeping backward and inward behind urogastric lobe, then turning outward and sweeping forward from behind epimeral peninsula, separating mesobranchial-epibranchial lobes and sweeping outward and forward to dorsal edge. Groove separating mesogastric from urogastric lobe indistinct on gastric ridge but continued onto epigastric lobe as better defined groove. Transverse shallow depression forms posterior edge of cardiac region separating it from intestinal lobe. Anteriorly a faint groove separates protogastric and hepatic lobes. Protogastric lobe surmounted by 3 moderately-sized and 1 tiny boss situated at anterodistal, proximomedial, posterodistal, and posterior parts of protogastric lobe. Hepatic lobe carries two marginal lobes separated by shallow depression. Mesogastric lobe has long, narrow anterior tongue which extends onto rostral area, apparently downturned into triangular rostrum and widens around anterior boss situated near anterior protogastric bosses to form a more or less continuous U-shaped arc with them; anterior process then narrows slightly but abruptly widens around base of triangular mesogastric lobe.

Scapular arch poorly delimited by shallow furrows. Gastric ridge barely differentiated by cervical furrow between mesogastric and urogastric lobes but better delimited by transverse extension of branchiocardiac groove behind urogastric lobe separating it from cardiac and intestinal lobes poorly dif-

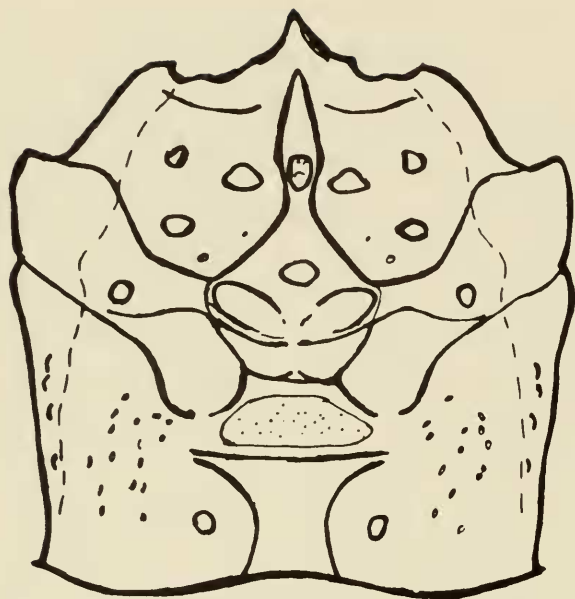


Fig. 3. Reconstruction of carapace of *Homolopsis centurialis*, new species, dorsal view.

ferentiated one from another. Branchial region differentiated into large, posterior metabranchial and mesobranchial lobe and well differentiated anterior epibranchial lobe. Mesobranchial lobe separated from epibranchial lobe by shallow groove. Epibranchial lobe inflated and ridge-like, forming epibranchial angle and widest portion of carapace, accentuated by curvature of cervical furrow around inner and anterior margin of epibranchial lobe. Two boss-like tubercles present on epibranchial lobe, one on dorsum and one on vertical wall of carapace. Metabranchial lobe arched with subtle ridge proximally carrying small boss and with 4 small marginal tubercles near middle; surface ornamented by coarse tuberculation. Carapace sides splayed outward along the linea homolica, leading to a misrepresentation of the dorsal morphology of this species which is idealized in Fig. 3.

Etymology.—Trivial name of binomen is taken from the Latin “centurialis,” meaning “of a hundred” in honor of its discovery during South Dakota’s centennial celebration.

Comparison.—*Homolopsis centurialis* is a typical homolopsid crab exhibiting most characteristics of the genus, including tumid



Fig. 4. Photograph of holotype of *Homolopsis centurialis*, new species, dorsal view, embedded in apatite concretion with sides of carapace splayed outward into plane of dorsum. (Scale = 1 cm)

areolations, boss-like projections on most lobes, and granulation over much of the carapace, all characteristics which easily distinguish *H. centurialis* from *H. williamsi* (Fig. 5a) and *H. glabra*. *Homolopsis centurialis* is most similar to *H. punctata* (Fig. 5c), from which it can be distinguished by its significantly different pattern of proto-gastric bosses in which the two anterodistal bosses are on a line parallel to the sagittal axis rather than on a line steeply inclined to the sagittal axis as in *H. punctata*, by having a differently-shaped cardiac region which is transverse and relatively short rather than diamond-shaped as in *H. punctata*, and by having relatively more poorly developed bosses than in *H. punctata*. *Homolopsis centurialis* is similar to *H. dispar* (Fig. 5e) in possessing relatively poorly developed bosses, but differs from that species by having a more poorly defined cervical groove on the sagittal ridge, being more granulate, by having a better developed boss on the anterior process of the mesogastric lobe, by having a significantly better developed boss on the proximal part of the epigastric lobe, and by lacking the well-developed epigastric bosses. *Homolopsis*

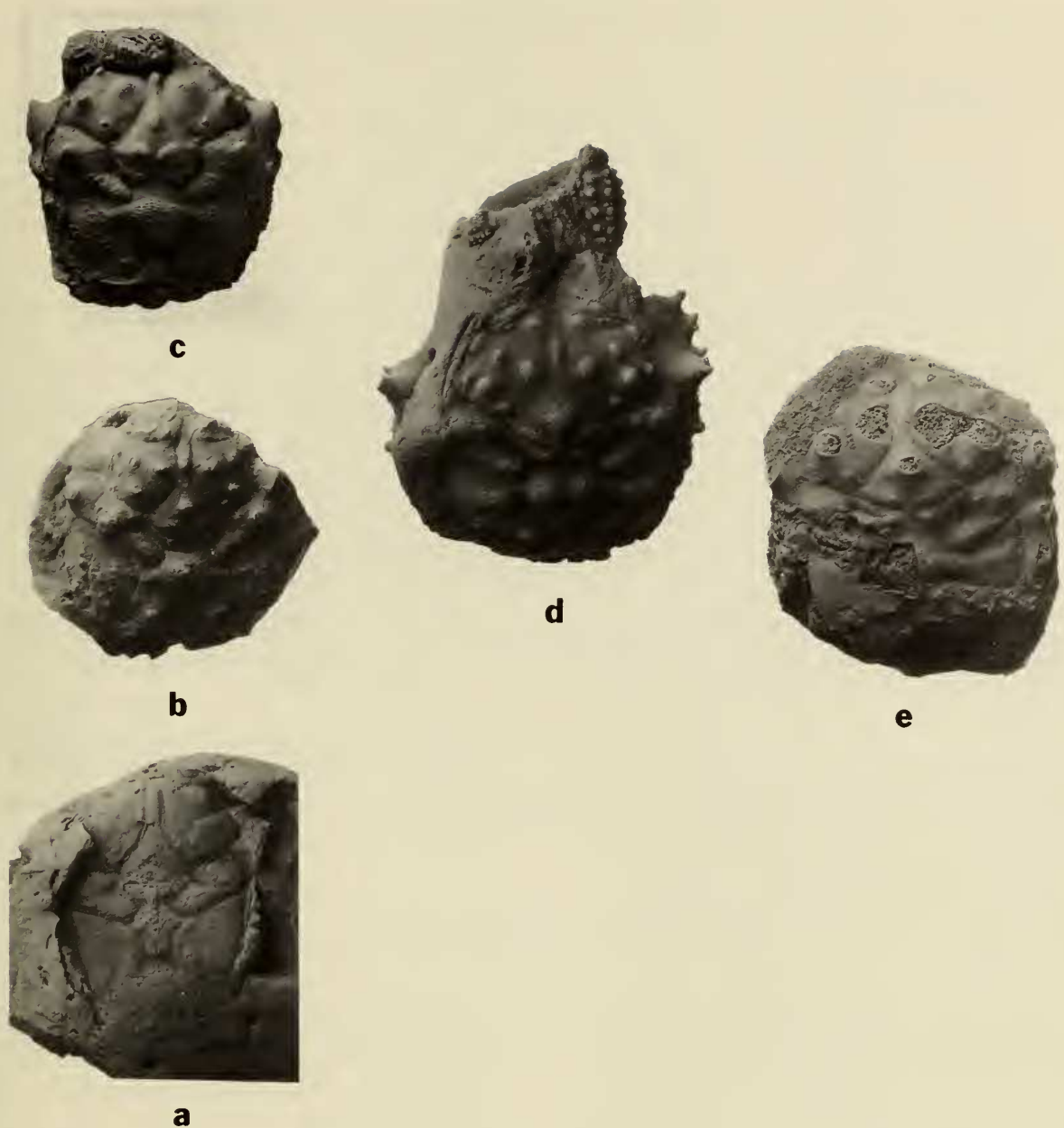


Fig. 5. North American species of *Homolopsis* Bell, 1863, arranged in stratigraphic sequence and approximate geographic position (left toward west, right toward east): Western Interior species; a, *Homolopsis williamsi*, new species; b, *H. centurialis*, new species; c, *H. punctata*, Rathbun, 1917; and Northern Atlantic Coastal Plain species; d, *H. atlantica*, Roberts, 1962; e, *H. dispar*, Roberts, 1962.

centurialis differs significantly from *H. atlantica* (Fig. 5d) by its less well-developed bosses, less tumid lobes, a more subdued anterolateral margin perhaps lacking the prominent anterolateral hepatic spines, by having four well developed protogastric bosses rather than the six, a continuous transverse cardiac lobe rather than the transversely-bilobed cardiac region, and the lack of a transverse metabranchial ridge.

Homolopsis centurialis is similar to *H.*

brightoni from which it is distinguished by being relatively longer, having a poorly differentiated protogastric lobe, and transversely-ridged cardiac lobe (rather than the diamond-shaped cardiac lobe of *H. brightoni*). *Homolopsis centurialis* differs significantly from *H. edwardsi* by being rectangular rather than oval, the small epibranchial spines, less developed posterolateral spination, and numerous differences in placement of the coarse ornamentation on the

various lobes (see also Carter 1898:21–22). *Homolopsis centurialis* differs from *H. tuberculata* Van Straelen, 1936 by having relatively reduced ornamentation, possessing a boss on the anterior process of the mesogastric lobe (lacking in *H. tuberculata*), and having a different pattern of protogastric bosses. *Homolopsis centurialis* differs from *H. schlueteri* (Beurlen, 1928 by being significantly shorter, by possessing a very different pattern of bosses, and by having differently shaped mesogastric and cardiac lobes. *Homolopsis centurialis* differs from *H. transiens* Segerberg, 1900 by possessing medial bosses on the mesogastric lobe lacking in *H. transiens*, by having a less developed cervical furrow across the gastric ridge, and a different distribution of bosses on the protogastric lobe. *Homolopsis centurialis* differs from *H. gibbosa* (also see Mertin 1941:230, fig. 25) by its posteriorly converging shape where *H. gibbosa* converges anteriorly, by having 4 protogastric bosses where *H. gibbosa* has 5 arranged in a different pattern, and by lacking the bilaterally arranged cardiac bosses of *H. gibbosa*.

Homolopsis centurialis differs from *Pithonoton planum* Van Straelen, 1936, and from *Prosopon schneideri* Stolley, 1924, by having a typically well-developed homolopsid morphology rather than prosoponid, although, as pointed out by Wright & Collins (1972:45), *P. planum* appears to be very close to the ancestral line leading to the homolopsids.

Paleogeography and Biostratigraphy of *Homolopsis*

The species assignable to the genus *Homolopsis* show an interesting pattern of development and evolution (Figs. 6, 7) indicating an origin in the northern Tethys Seaway in the Neocomian (Early Cretaceous) possibly from prosoponid ancestors. Glaessner (1969:R490) briefly summarized the systematics of the Homolidae and provided an illustration of a possible Jurassic

ancestor, ?*Titanohomola*, Glaessner, 1933. Wright & Collins (1972:45) suggested that *Pithonoton planum* Van Straelen (1936:27, Pl. 4, fig. 1) and *Prosopon schneideri* Stolley (1924:413, Pl. 13, fig. 1) were close to ancestral forms for *Homolopsis* and, particularly, *P. planum* was cited as a possible “young specimen of an ancestral *Homolopsis*, distinguished from *H. glabra* mainly by the stronger median furrow on the urogastric lobe and stronger cardiac tubercles.” Although I have not seen the specimens representing *P. planum*, Van Straelen’s figures (1936:Pl. 4, figs. 1, 2) certainly force me to concur with Wright & Collins. Three distinct lineages of homolid crabs were derived from the early ancestors of the homolids by the Albian; those assignable to *Homolopsis*, to *Zygastrocarcinus* Bishop 1983, and the aberrant Australian species *Homolopsis? spinulosa*. The species of *Homolopsis* migrated and evolved in the shallow waters of the northern Tethys in northern Europe (*H. gibbosa*, *H. schneideri*, and *H. transiens*), the Northern Atlantic Coastal Plain (*H. atlantica* and *H. dispar*), and in the Western Interior of the USA (*H. williamsi*, *H. centurialis*, and *H. punctata*) (Bishop, 1986b). Members of the genus *Zygastrocarcinus* [*Z. etheridgei* (H. Woodward, 1892); *Z. mendryki* (Bishop, 1982); *Z. griesi* Bishop, 1983; *Z. richardsoni* (Woodward, 1896); *Z. japonica* Yokoyama, 1911; and *Z. gorrelli* (Rathbun, 1926)], have a more western Tethys (i.e., Tethyan-Pacific) distribution overlapping that of *Homolopsis* in the Western Interior Seaway. *Homolopsis? spinulosa* from the Upper Cenomanian of Australia probably represents a third lineage of Cretaceous homolid evolution, one which apparently went rapidly to extinction.

The pattern of evolution of *Homolopsis* s.s. is one of initial development in the Neocomian in Central and Northern Europe, emigration and adaptive radiation in the shallow waters of southern England, followed by emigration and speciation in

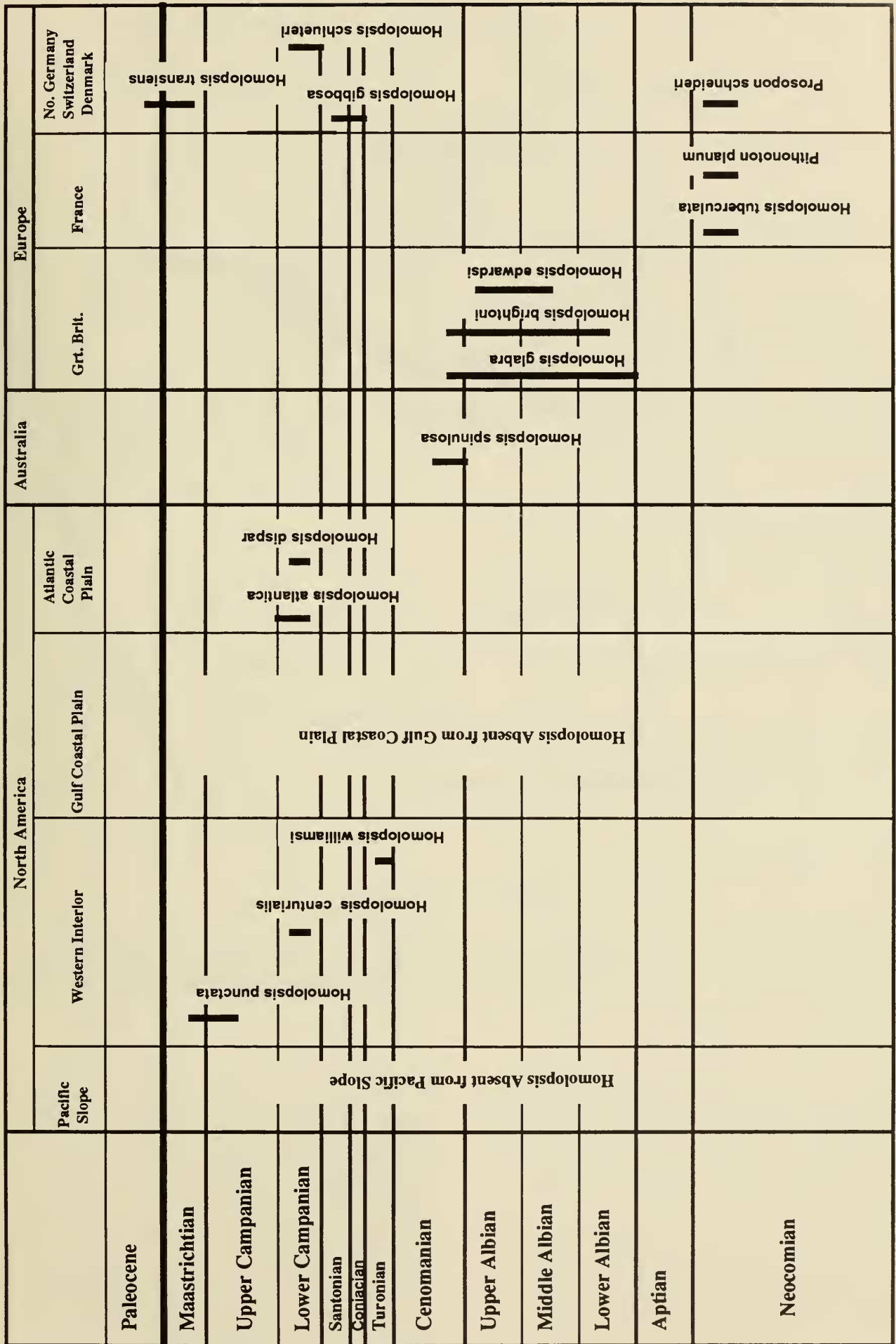


Fig. 6. Stratigraphic range chart showing ranges and biogeographic positions of species of *Homolopsis*, Bell, 1863, and closely related prosoponids.

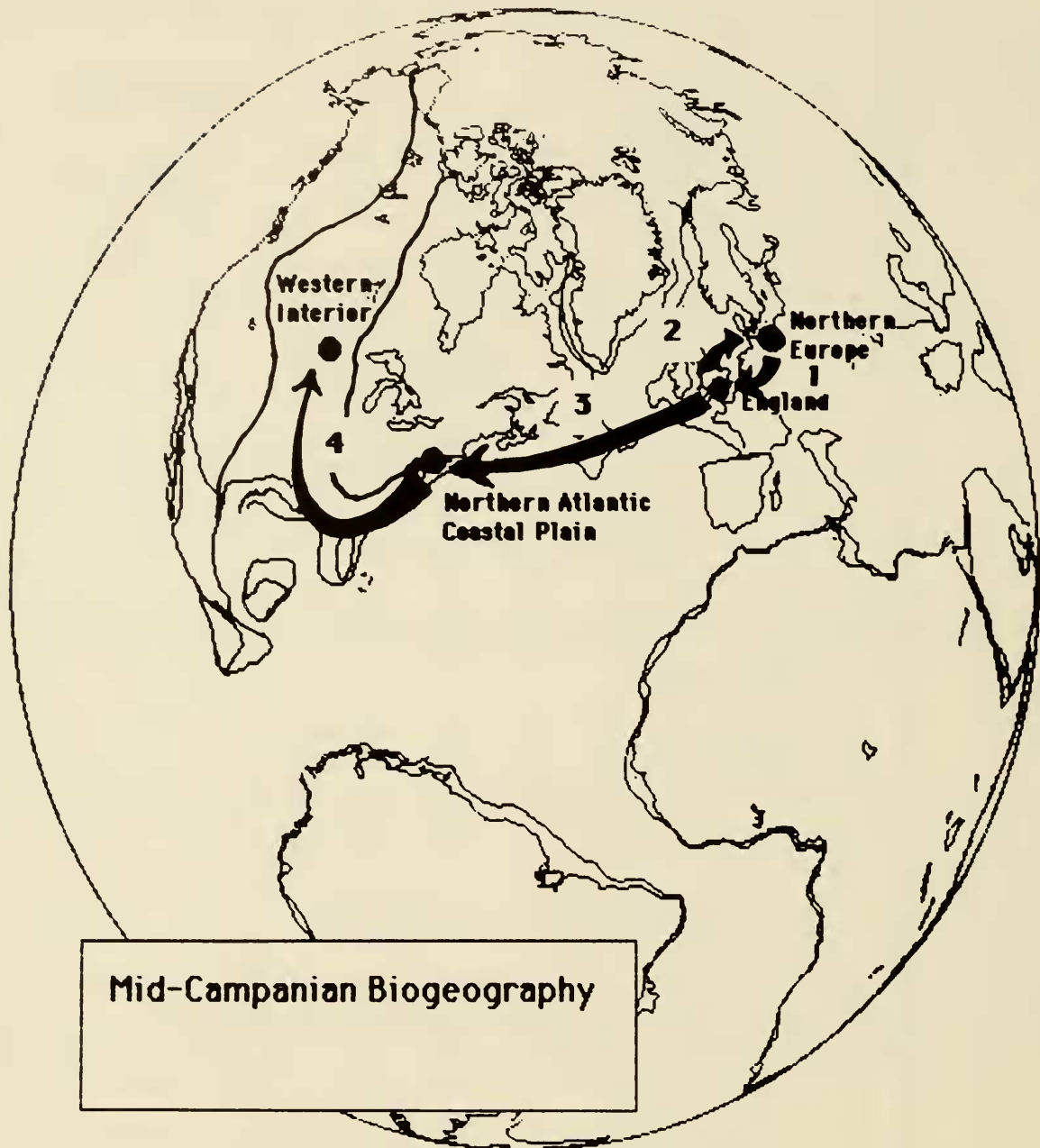


Fig. 7. Late Cretaceous paleogeography illustrating the wave-like pattern of emigrations of *Homolopsis*, Bell, 1863, from Central Europe into Great Britain (Southern England) (1) and subsequently into Northern Europe (2), the Northern Atlantic Coastal Plain of the United States (3), and the Western Interior Seaway of the United States (4).

Northern Europe, the Northern Atlantic Coastal Plain, and the Western Interior Seaway. Only *H. transiens* is known to have survived the mass extinctions at the Cretaceous-Tertiary boundary. No other record of Cenozoic species of *Homolopsis* is known.

The modern homolids *Homola* and *Latreillia* are deep-water forms. The carapace similarity between the typical fossil species of *Homolopsis* and the Recent *Homola bar-*

bata (Fabricius, 1793) is truly remarkable, strongly suggesting that *Homola* is a direct descendent of one of the Cretaceous species of *Homolopsis*. This pattern of retreat into deep water refugia is seen in other decapod taxa (e.g., linuparid lobsters, retroplumid crabs) and would account for the sparse record of Cenozoic forms because of the relative lack of preservation of deep water sediments in the geologic record.

Acknowledgments

I extend sincere thanks to Chance and Cindy Davis for granting permission to collect on the Heart Tail Ranch and to Norman Durr for permission to collect on his land north of Belle Fourche. Special acknowledgment is made to all those assisting me in the field and helping slowly build the collection upon which this research is based. Direct support for this research has been received from the Committee for Research and Exploration, National Geographic Society, the Faculty Research Committee, Georgia Southern University, and the Museum of Geology, South Dakota School of Mines. Rodney Feldmann read the original manuscript and strengthened it with his suggestions.

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